

Evolutionary Explanations for Cooperation Review

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Natural selection favours genes that increase an organism's ability to survive and reproduce. This would appear to lead to a world dominated by selfish behaviour. However, cooperation can be found at all levels of biological organisation: genes cooperate in genomes, organelles cooperate to form eukaryotic cells, cells cooperate to make multicellular organisms, bacterial parasites cooperate to overcome host defences, animals breed cooperatively, and humans and insects cooperate to build societies. Over the last 40 years, biologists have developed a theoretical framework that can explain cooperation at all these levels. Here, we summarise this theory, illustrate how it may be applied to real organisms and discuss future directions.

The Problem of Cooperation

A behaviour is cooperative if it provides a benefit to another individual and if it has evolved at least partially because of this benefit [1]. Such behaviours pose a problem to evolutionary theory because — all else being equal — they would reduce the relative fitness of the performer of that behaviour and hence be selected against [2] (Figure 1). To give a specific example, consider the star of many a nature documentary, the meerkat. Meerkats generally live in groups of up to 30 adults with their young. The adults of a group can be divided into the dominant male and female, who do most of the breeding, and the subordinates, who help the dominants raise their offspring [3]. When one of these subordinates has found a tasty scorpion, why should it hand it over to one of the offspring produced by the dominant pair? How can we reconcile this behaviour with selfish interests, even at the level of the gene, and the Darwinian struggle for survival and reproduction in the natural world?

This problem also applies to economics and human morality, with a famous example being the 'tragedy of the commons' [4]: imagine a number of shepherds, each deciding how many sheep to keep on a shared pasture. The addition of extra sheep will have both a benefit and a cost. The benefit is that the shepherd will gain from extra sheep. The cost is potential overgrazing, which can damage the pasture. However, whilst our focal shepherd gains all of the benefit, he pays only a fraction of the cost, which is shared between all of the shepherds. Consequently, the individual shepherd has more to gain than to lose from adding extra sheep. The tragedy is that — as a group — all the

shepherds would benefit from grazing less sheep. Such cooperation, however, is not stable, because each individual can gain by selfishly pursuing their own interests.

Most attention on the problem of cooperation (see Box 1 for glossary) has been focused on interactions between animals. However, the same problem occurs at all levels of biological organisation [2,5–7]. The very existence of multicellular organisms relies upon cooperation between the eukaryotic cells that make them up. The mitochondria upon which these eukaryotic cells rely were once free-living prokaryotic cells but now live cooperative lives. Separate genes, which make up the genome, cooperate in what has been termed the 'parliament of the genes' [8]. The tree of life is dominated by single-celled microorganisms that appear to perform a huge range of cooperative behaviours [9]. For example, the growth and survival of bacteria depend upon excreted products that perform a variety of functions, such as scavenging nutrients, communication, defence and movement. The benefits of such extracellular products can be shared by neighbouring cells and hence they represent a 'public good' that is open to the problem of cooperation [9]. Almost all of the major evolutionary transitions from replicating molecules to complex animal societies have relied upon solving the problem of cooperation being solved [7].

The Solutions

As cooperation is in evidence throughout the natural world, there must be a solution to the problem. Theoretical explanations for the evolution of cooperation (or any behaviour) are broadly classified into two categories: direct fitness benefits or indirect fitness benefits [2,10–12] (Figure 2). This follows from Hamilton's [2] insight that individuals gain inclusive fitness through their impact on the reproduction of related individuals (indirect fitness effects) as well as through their impact on their own reproduction (direct fitness effects) (Figure 3). The importance of Hamilton's work cannot be overstated — it is one of the few truly fundamental advances since Darwin in our understanding of natural selection.

A cooperative behaviour yields direct fitness benefits when the reproductive success of the actor, who performs the cooperative behaviour, is increased. Cooperative behaviours that benefit both the actor and the recipient(s) of the behaviour are termed 'mutually beneficial' [1]. A cooperative behaviour can be explained by indirect fitness benefits if it is directed towards other individuals who carry the gene for cooperation [2]. This is usually termed 'kin selection' [13], because the simplest and most common way this could occur is if cooperation is directed at relatives, who share genes from a common ancestor [11]. By helping a close relative reproduce, an individual is still passing copies of its genes on to the next generation, albeit indirectly. Cooperative behaviours that are costly to the actor and beneficial to the recipient are termed 'altruistic' [2] and can only be explained by indirect fitness benefits. A key point here is that we are

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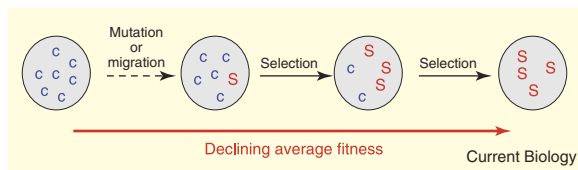


Figure 1. The problem of cooperation.

In the absence of one of the mechanisms discussed in this review, natural selection favours selfish individuals who do not cooperate. Consider a population of cooperators ('C') in which an uncooperative, selfish cheater ('S') arises through mutation or migration. In a mixed population, the selfish cheater benefits from the cooperative behaviour of the cooperators, without paying the cost. Consequently, the selfish cheater has a higher fitness than the cooperators and spreads through the population, despite the fact that this leads to a decline in mean fitness. (Redrawn after [104].)

considering the average consequences of a behaviour and not the consequences of every single instance.

Kin Selection and Indirect Fitness Benefits

Hamilton's inclusive fitness (kin selection) theory shows how altruistic cooperation can be favoured between relatives. This is encapsulated in a pleasingly simple form by Hamilton's rule [2], which states that a behaviour or trait will be favoured by selection, when $rb - c > 0$, where c is the fitness cost to the actor, b is the fitness benefit to the recipient, and r is their genetic relatedness. Putting this inequality into words, altruistic cooperation can therefore be favoured if the benefits to the recipient (b), weighted by the genetic relatedness of the recipient to the actor (r), outweigh the costs to the actor (c). This follows from inclusive fitness theory because $-c$ represents the direct fitness consequences of a social behaviour and rb the indirect fitness consequences. Hamilton's rule predicts greater

levels of cooperation when r or b are higher and c is lower.

Explanations for cooperation based on indirect fitness benefits, i.e. kin selection, require a sufficiently high genetic relatedness (r) between interacting individuals. The coefficient of relatedness (r) is a statistical concept, describing the genetic similarity between two individuals, relative to the average similarity of all individuals in the population [11]. Hamilton [2] suggested two possible mechanisms through which a high relatedness could arise between social partners: kin discrimination and limited dispersal.

Kin Selection and Kin Discrimination

The first mechanism for generating sufficiently high relatedness to make kin selection viable is kin discrimination, when an individual can distinguish relatives from non-relatives and preferentially direct aid towards them (nepotism) [2]. This has been demonstrated in several cooperatively breeding vertebrates, such as long-tailed tits [14], where individuals that fail to breed independently help at the nest of closer relatives [14] (Figure 4A). In this species, individuals distinguish between relatives and non-relatives on the basis of vocal contact cues, which are learned from adults during the nesting period (associative learning) [15]. This leads to a situation in which individuals tend to help relatives whom they have been associated with during the nestling phase.

Kin selection theory also explains the variation in the level of kin discrimination across species [16]. In contrast to the long-tailed tits, other cooperatively breeding vertebrates, such as meerkats [17], do not show kin discrimination when helping. The advantage of kin discrimination will be positively correlated with the extent of the benefit (b) provided by helping. In the extreme, if

Box 1

Glossary.

Actor: the focal individual performing a behaviour.

Altruism: a behaviour that is costly to the actor and beneficial to the recipient. Cost and benefit are defined on the basis of the lifetime direct fitness consequences of a behaviour.

Cheaters: individuals who do not cooperate or who cooperate less than their fair share, but are potentially able to gain the benefit of others cooperating.

Cooperation: a behaviour that provides a benefit to another individual (recipient), and the evolution of which has been dependent on its beneficial effect for the recipient.

Direct fitness: the component of fitness gained from producing offspring; the component of personal fitness due to one's own behaviour.

Greenbeard: a hypothetical gene that causes in carriers both a phenotype that can be recognised by conspecifics (a 'green beard') and a cooperative behaviour towards conspecifics who show a green beard.

Inclusive fitness: "the effect of one individual's actions on everybody's numbers of offspring [...] weighted by the relatedness [10]; the sum of direct and indirect fitness; the quantity maximised by Darwinian individuals.

Indirect fitness: the component of fitness gained from aiding related individuals.

Kin selection: process by which traits are favoured because of their beneficial effects on the fitness of relatives.

Mutual benefit: a benefit to both the actor and the recipient.

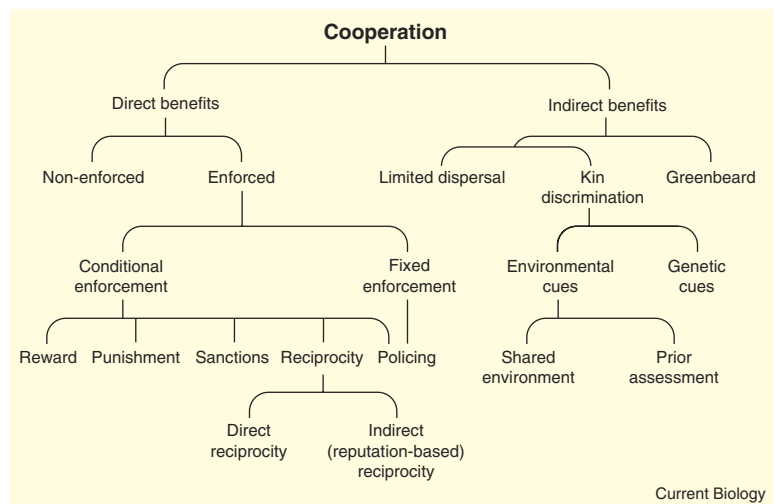
Mutualism: two-way cooperation between species.

Recipient: an individual who is affected by the behaviour of the focal individual.

Relatedness: a measure of the genetic similarity of two individuals, relative to the average; the statistical (least-squares) regression of the recipient's breeding value for a trait on the breeding value of the actor.

Figure 2. A classification of the explanations for cooperation.

Direct benefits explain mutually beneficial cooperation, whereas indirect benefits explain altruistic cooperation. Within these two fundamental categories, the different mechanisms can be classified in various ways [1,12,55,72]. These possibilities are not mutually exclusive; for example, a single act of cooperation could have both direct and indirect fitness benefits or interactions with relatives could be maintained by both limited dispersal and kin discrimination. Our dividing up of conditional enforcement strategies is for illustration only, a detailed discussion is found elsewhere [72].



a supposedly 'helping' behaviour provides little or no benefit to its recipients, then there is little or no advantage in directing it towards closer relatives. This leads to the prediction that the extent of kin discrimination should be greater in species where a greater fitness benefit is derived from receiving help — a pattern indeed observed across cooperatively breeding vertebrate species [16] (Figure 5). Overall, the benefit that helping brings to the recipient can explain 42% of the variation in the extent of kin discrimination across species.

Kin discrimination has also been found in species that are not usually thought of from a social perspective. *Dictyostelium purpureum* is a unicellular slime mould found in forest soils [18]. When starved of its bacterial food source, the cells of this species aggregate in thousands to form a multicellular, motile 'slug'. Slugs migrate to the soil surface, where they transform into a fruiting body composed of a stalk structure holding aloft a ball of spores. The non-viable stalk cells are sacrificed to aid the dispersal of the spores. This requires explanation because cooperative cells that form stalk cells could be exploited by cheaters who avoid the stalk and instead migrate to form spores in the fruiting body. Kin selection offers a potential solution to this problem, because stalk cells could gain an indirect fitness benefit from helping relatives disperse. This suggests that it would be advantageous for the individual amoebae to preferentially form a slug with relatives. Indeed, kin discrimination during slug formation has recently been observed in *D. purpureum* [18]. Specifically, when two lineages are mixed and allowed to form slugs on agar plates, they discriminate to the extent that the average relatedness in fruiting bodies increases to a value of 0.8, as opposed to the expected value of 0.5 (Figure 4B).

Kin Discrimination Cues

Kin discrimination can occur through the use of environmental or genetic cues [19]. The most common mechanism appears to involve environmental cues, such as prior association or shared environment, as in long-tailed tits and a range of other animals from humans to ants [20,21]. In contrast, in the case of the

slime mould some genetic cue of relatedness is likely to be involved — also termed 'kin recognition', 'genetic similarity detection', 'matching' or 'tags'. In order to detect genetic similarity, an individual must have some cue that is genetically determined — such as the cuticular hydrocarbon profile of an insect [22], or the odour produced by scent glands in a mammal [23] — and a 'kin template' for comparison [19]. This kin template could be determined by the individual's own genotype or cues ('self-matching') and/or through learning the cues of its rearing associates [23].

Kin discrimination based on genetic cues is often unlikely to be evolutionarily stable. The reason is that recognition mechanisms require genetic variability (polymorphism) in order to provide a cue. However,

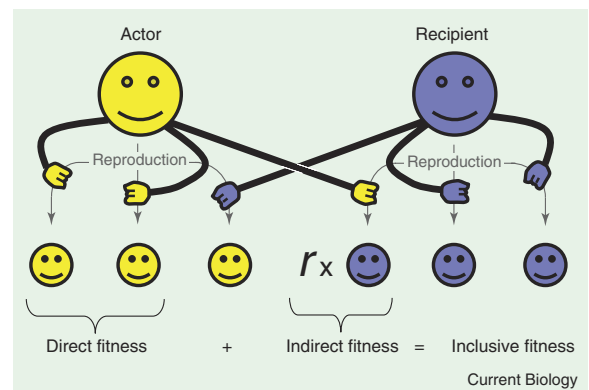


Figure 3. Inclusive fitness and cooperation.

Inclusive fitness is the sum of direct and indirect fitness [2]. Social behaviours affect the reproductive success of self and others. The impact of the actor's behaviour (yellow hands) on its reproductive success (yellow offspring) is the direct fitness effect. The impact of the actor's behaviour (yellow hands) on the reproductive success of social partners (blue offspring), weighted by the relatedness (r) of the actor to the recipient, is the indirect fitness effect. Inclusive fitness does not include all of the reproductive success of relatives (blue offspring), only that which is due to the behaviour of the actor (yellow hands). Also, inclusive fitness does not include all of the reproductive success of the actor (yellow offspring), only that which is due to its own behaviour (yellow hands).

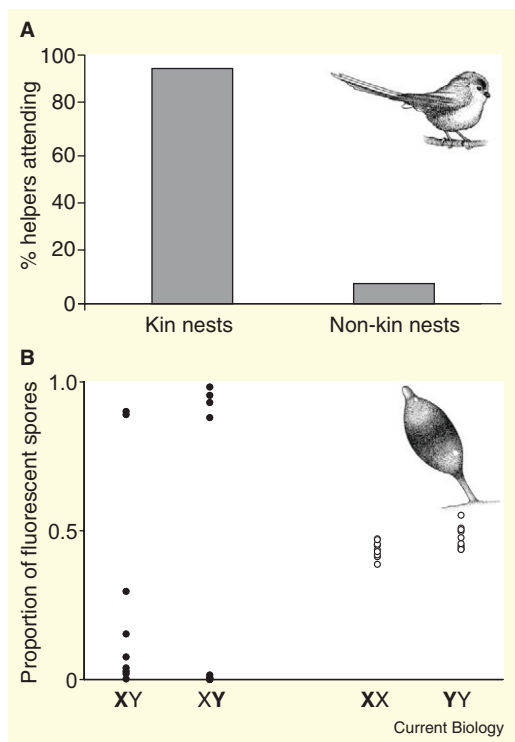


Figure 4. Kin discrimination.

(A) Kin discrimination in long-tailed tits. 96% of helpers prefer to help at nests containing related chicks when they have the choice of where to invest their efforts. With permission from [14]. (B) Kin discrimination in the unicellular slime mold *Dictyostelium purpureum* (social amoebae) [18]. A scatter plot shows the proportion of fluorescently labelled spores in fruiting bodies when two isolates are placed together at equal proportions and one is fluorescently labelled (bold). There is a greater variance in the experimental treatment where the two isolates are different lineages (X and Y), than in the control treatment where the isolates are the same lineage. This shows that individuals preferentially form fruiting bodies with members of their own lineage. With permission from [18].

individuals with common genetic variants would be more likely to be helped, and thus more common genes would be driven to fixation [24]. Consequently, kin discrimination is, as it were, its own worst enemy,

eliminating the genetic variability that it requires to work. Thus, kin discrimination based on genetic cues is often not found where it might be expected [25–28]. In cases where kin discrimination based upon genetic cues has been observed, it can usually be argued that there is some other selective force maintaining variability at the recognition loci, such as host-parasite co-evolution in the major histocompatibility complex (MHC) of vertebrates [24]. Cue diversity may also be maintained if there is limited dispersal, such that interactants tend to be relatives anyway [24,29], as is likely to be the case with the slime mould discussed above.

Green Beards

Indirect fitness benefits will also be obtained if cooperation is directed towards non-relatives who share the same cooperative gene [2,30]. Dawkins [31] illustrated this with a hypothetical example of a gene that gave rise to green beards, while simultaneously prompting individuals with green beards to preferentially direct cooperation towards other green-bearded individuals. This mechanism can also occur without a visible tag — for example, if the cooperative gene also caused some effect on habitat preference that led to individuals who carried that gene settling together [30]. Consequently, although this mechanism is usually termed a 'greenbeard', it more generally represents an assortment mechanism, requiring a single gene — or a number of tightly linked genes — that encodes both the cooperative behaviour and causes cooperators to associate [12].

Greenbeards are likely to be rare, because cheaters that display the green beard, or assorting behaviour, without also performing the cooperative behaviour, could invade and overrun the population. Furthermore, in the absence of relatedness over the whole genome, the altruistic greenbeard would be in conflict with genes elsewhere in the genome, where there would be strong selection for suppression of the greenbeard [32,33]. One of the few cases where a cooperative greenbeard occurs is in the slime mould *Dictyostelium discoideum*, which forms fruiting bodies in a very similar way to *D. purpureum*. In *D. discoideum*, individual amoebae with the *csa* cell-adhesion gene adhere to each other in aggregation streams and cooperatively

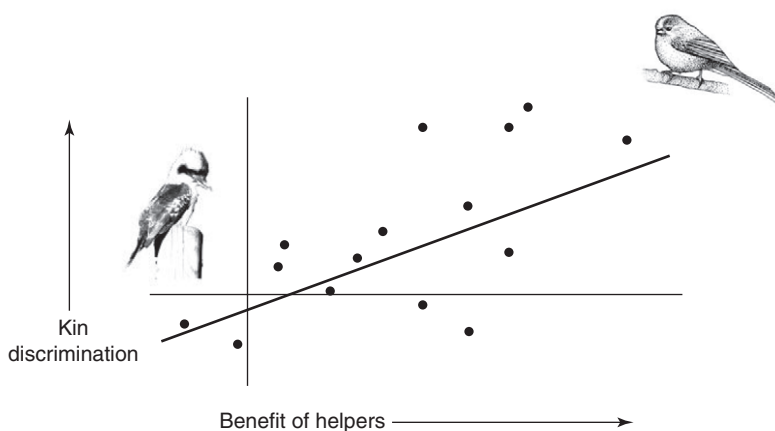


Figure 5. Kin discrimination and the benefit of helping.

Across cooperatively breeding bird and mammal species, helpers are more likely to discriminate in favour of relatives when the amount of help they provide increases the survival of offspring to the following year. The extent to which individuals preferentially help closer relatives (kin discrimination) is plotted against the benefit of helping. The significant positive relationship between these two variables is predicted by kin selection theory. The illustration shows the laughing kookaburra, a species which does not show kin discrimination in its helping behaviour. Modified with additional data points from [16].

form fruiting bodies at the exclusion of *csa* mutants [34]. It is perhaps not surprising that greenbeards should be rare, given that the idea was not developed as a theory to explain altruism, but as a thought experiment to show that genetic relatedness — rather than genealogical relationship *per se* — is the key to kin selection.

Kin Selection and Limited Dispersal

Limited dispersal (population viscosity or structure) can generate high degrees of relatedness between interacting individuals because it will tend to keep relatives together [2,5]. In this case, altruism directed indiscriminately at neighbours could be favoured, because those neighbours are more likely to be relatives. This mechanism has the potential to be important in a wide range of organisms because it does not require any mechanism of kin discrimination. Instead, all that is required is that the level of cooperation evolves in response to the mean relatedness between individuals who tend to interact by chance.

The predicted role of limited dispersal has been supported by an experimental evolution study on cooperation in bacteria [35]. Many bacteria release siderophore molecules to scavenge for iron. These represent a cooperative public good: they are costly to the individual to produce, but iron bound to siderophores can be taken up by any cell, providing a benefit to other individuals in the locality. When populations of the bacterium *Pseudomonas aeruginosa* containing a mixture of a wild-type strain that produces siderophores and a cheater mutant that does not were maintained in conditions that led to relatively high or low relatedness [35], the cooperative wild-type strain out-competed the cheater mutant strain only under conditions of relatively high relatedness (Figure 6). More generally, limited dispersal is likely to be important for maintaining a range of public goods produced by bacteria to help with the gathering of resources, growth and reproduction [9].

Limited Dispersal and Kin Competition

Although limited dispersal can favour cooperation, it will not necessarily do so [36]. The problem is that, although limited dispersal can bring relatives together to cooperate, it can also keep them together to compete [30,37]. This competition between relatives can reduce or even completely remove selection for cooperation between relatives. One way of thinking about this is that the concomitant competition reduces the benefit (*b*) of helping relatives [11]. In the extreme case, there is no point helping a brother, if their increase in fitness comes at the cost of another brother's reproductive success [38]. In the simplest possible scenario, the effects of increased relatedness and increased competition exactly cancel out, such that limited dispersal has no influence on the evolution of cooperation [39]. However, a number of factors, which are likely to be biologically important, can reduce the competition between relatives and hence allow limited dispersal to favour cooperation [36]. For example, when cooperation allows population expansion (as with bacterial public goods), when relatives tend to disperse together ('budding viscosity') or when the lifecycle involves a

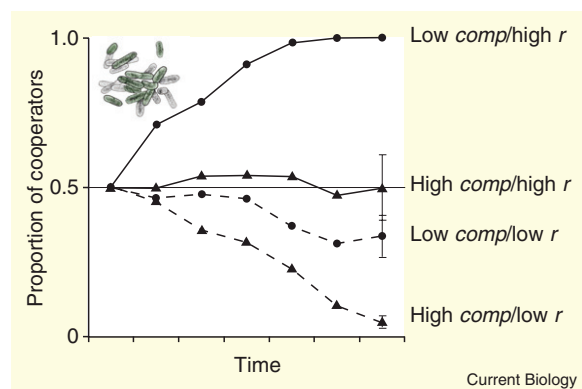


Figure 6. Relatedness, competition and cooperation.

An experimental study on cooperative siderophore production in the bacteria *Pseudomonas aeruginosa* has shown how selection for cooperation is influenced by relatedness and the extent of competition between relatives [35]. The proportion of cooperative individuals who produce siderophores is plotted against time. The different lines represent relatively high (solid lines) and low (dashed lines) relatedness. The different symbols represent relatively low (circle) and high (triangle) amounts of competition between relatives. Cooperation is favoured by higher relatedness and lower competition between relatives. With permission from [35].

period of interaction with close relatives followed by a period of dispersal before competition ('alternating viscosity') [39–41].

Although it has received little empirical attention [38], some experimental support for how competition between relatives can select against cooperation between relatives comes from the experiment with *P. aeruginosa* on siderophore production described above [35]. Relatively low competition between relatives was induced by allowing more productive groups to make a greater contribution to the next generation, thereby minimising local competition within groups. Relatively high competition between relatives was obtained by making all groups contribute equally to the next generation and hence making local competition between groups more important. As predicted by theory, the cheater mutant strain was able to spread to a higher proportion of the population when there was greater competition between relatives (Figure 6). More recently, it has also been realised that local competition for resources not only selects against cooperation, but it can select for individuals to spitefully harm less related individuals [42], such as when the soldier larvae of polyembryonic wasps attack and kill larvae to which they are less related [43,44].

Don't Forget *b* and *c*

There is often an overemphasis — both conceptually and empirically — on the importance of the relatedness term (*r*) in Hamilton's rule and a corresponding neglect of the benefit (*b*) and cost (*c*) terms [45,46]. To some extent, this is the case because genetic similarity can be measured more easily than components of fitness. However, focusing too strongly on *r* can lead to misunderstanding and confusion, because variation in *b* and *c* can be equally important. One of the clearest cases of such confusion arises from a consideration of why

eusociality has evolved so many times in the haplodiploid Hymenoptera — the ants, bees and wasps. Hamilton [2,5] originally suggested that this was the case because their haplodiploid genetics leads to female workers being more related to their sisters ($r = 0.75$) than to their offspring ($r = 0.5$) and hence provided a relatedness benefit that predisposed them to the evolution of cooperation. However, it was later shown that this higher relatedness to sisters was exactly cancelled by a lower relatedness to brothers ($r = 0.25$) relative to sons ($r = 0.5$) [47]. Consequently, it has long been assumed that the high frequency of eusociality in the Hymenoptera is due to factors that provide a high benefit-to-cost-ratio (b/c), such as nest building, stinging and common parental care [48,49]. However, the misconception that kin selection only predicts that r is important still arises [50], whereas in reality, it predicts that r , b and c are important [51].

The importance of b has been discussed above with respect to selection for kin discrimination and the benefit of helping [16] (Figure 5), and how selection for cooperative siderophore production is reduced by local competition between relatives [35] (Figure 6). An elegant example of the importance of the cost of helping (c) is provided by field experiments on the hairy-faced hover wasp [52]. In nests of this species, one to ten related females form an orderly queue to reproduce. The dominant female lays the eggs and the subordinate females forage and tend the young. High-ranked subordinates were experimentally removed from the nest, hence moving the remaining subordinates to a higher position in the queue. This increases the relative cost of helping, because it is more likely that the subordinate will succeed to the breeding position and so energy expended on foraging could reduce resources available for breeding, as well as decreasing the likelihood of surviving to gain the breeding position. As predicted by kin selection theory [53], when individuals were moved up the queue, they reduced the number of foraging trips [52]. This illustrates that, as the cost of helping increased, individuals cooperated less.

Direct Fitness Benefits

The evolution of cooperation does not only depend upon kin selection and indirect fitness benefits — cooperation can also provide a direct fitness benefit to the cooperating individual [54]. In this case, cooperation is mutually beneficial and not altruistic [1]. We divide the direct fitness explanations for cooperation into two categories (Figure 2). First, cooperation may provide a benefit, as a by-product, or automatic consequence, of an otherwise 'self-interested' act [45,55]. For example, cooperation could lead to an increase in group size, which increases the survival of everyone — including the individual who performs the cooperative behaviour — due to larger groups being better at avoiding predators or competing with other groups [56]. Second, there may be some mechanism for enforcing cooperation by rewarding cooperators or punishing cheaters [57]. It can also be useful to distinguish enforcement mechanisms that are behaviourally inflexible from those that are adjusted conditionally in response to the level of cooperation. In the latter case, the benefit to the actor depends upon the

recipient adjusting their behaviour towards the actor in response to the actor's behaviour.

By-Product Benefits

Cooperation may provide some automatic benefit without enforcement. One way this could occur is if members of a group have some shared interest in cooperation. In many cooperatively breeding vertebrates — such as meerkats — a larger group size can provide a benefit to all the members of the group through an increase in survival, foraging success or the likelihood of winning conflicts with other groups [58]. In such a case, subordinate individuals can be selected to help rear offspring that are not their own, in order to increase group size — a process termed 'group augmentation' [56]. Selection for such helping is further increased if there is a chance that the subordinate will obtain dominance in the group at some later point, because they would then have a larger number of helpers themselves. The advantages of group augmentation would be greatest for the sex that is most likely to remain and breed in the natal group, which provides an explanation for why the level of helping is greatest in that particular sex for birds and mammals [59]. Similar benefits of increased individual success in larger groups have been suggested to be important in other cooperative organisms, such as ants and social spiders [60,61]. Things can get more complicated if the individuals in the group are related, because then by-product benefits can at the same time provide indirect fitness benefits, either because the actor helps a relative [56] or because the by-product benefits are shared with relatives [62].

Direct fitness benefits also play a role in cooperative breeding in the wasp *Polistes dominulus* [63]. In this species, colonies are initiated by one or a few foundress females that form a dominance hierarchy with the dominant laying most of the eggs and the subordinates carrying out most of the more risky foraging. It was found that 35% of subordinates were unrelated to the dominant female. These subordinates gain significant direct fitness benefits from staying and helping on the nest because dominants suffer an appreciable mortality, and so there is approximately a 10% chance that a subordinate will have become the dominant in the group by the time the workers emerge [63]. It is unlikely that subordinates are merely helping non-relatives by accident, because there is sufficient between-individual variation in cuticular lipids to allow subordinates to distinguish relatives from unrelated nest-mates [64]. Thus, selection could have acted to reduce or remove cooperative behaviour when subordinates form a colony with non-relatives.

Enforced Cooperation

Cooperation can be enforced if there is a mechanism for rewarding cooperators or punishing cheaters [54,57,65]. Trivers [54] emphasised that cooperation could be favoured in reciprocal interactions with individuals preferentially aiding those that have helped them in the past. In this case, cooperation provides a direct fitness benefit, as it is only favoured if the short term cost of being cooperative is outweighed by the long term benefit of receiving cooperation [1,12].

Trivers termed this 'reciprocal altruism', but because it provides a direct fitness benefit, it is mutually beneficial and not altruistic. Consequently, reciprocity [66] or reciprocal cooperation [65] are more appropriate terms [1]. Here, we use the term reciprocity to refer to cooperation preferentially directed at cooperative individuals, either directly ('help those that help you') or indirectly ('help those that help others') [54,67,68].

Although such reciprocity has attracted a huge amount of theoretical attention, it is thought to be generally unimportant outside of humans [69–71]. Our use of the term 'reciprocity' differentiates it from other cases of enforcement that also rely on behavioural flexibility and that have been variously termed 'punishment', 'policing', 'sanctions', 'partner-switching' and 'partner choice' [1,55,57,72] (Figure 2). It is beyond the scope of this review to sort the relationships between these different mechanisms [72]. In some cases, the term 'reciprocity' is used more generally to cover all these instances [12].

Enforcement has been suggested to be important in a number of vertebrate species. One example is found in meerkats, where the dominant female suppresses reproduction in her subordinates [73]. If a subordinate female becomes pregnant when the dominant is also pregnant, then the dominant is likely to subject the subordinate to aggressive attack and temporarily evict her from the group, which usually leads to abortion of the subordinate's litter. Enforcement has also been suggested to be an important selective force for cooperation in humans. In one study, students were split into groups of four to play a public goods game for cash prizes, where each person could contribute monetary units to a group project [74]. The experiment was repeated with and without punishment; punishment was incorporated by allowing individuals to pay money to have units deducted from other players, after they were informed about each other's investments. As expected, punishment led to higher levels of cooperation [74] (Figure 7A).

Enforcement can also explain cooperation between species. An elegant example is provided by the cleaner fish *Labroides dimidiatus*, which removes and eats ectoparasites from its client reef fish. Although parasite removal and food acquisition are clearly beneficial to the client and cleaner, respectively, there is a conflict, because the cleaners would prefer to eat the tissue or mucus of their hosts, which is costly to the host [75]. The clients use three mechanisms to suppress this conflict and enforce cooperative feeding on ectoparasites only: avoiding cleaners that they have observed cheating (partner choice), leaving for another cleaner (partner switching), and aggressively chasing the cleaner (punishment) [75,76]. Observational and experimental data suggest that cleaner fish are more cooperative and less likely to feed on mucus after punishment [75,76].

Why Enforce?

Whilst it is clear that behaviours such as punishment or policing favour cooperation, it is sometimes less obvious why they will be favoured by selection. In order to be favoured, such behaviours must provide a direct or an indirect fitness benefit to the punisher [77,78]. The

simplest way in which they could provide a direct fitness advantage is if the behaviours led to the termination of interactions with relatively uncooperative individuals (ostracism) and hence allowed interactions to be focused on more cooperative individuals [57,65,79–81]. This mechanism appears to be operating in the cleaner fish discussed above, the legume-rhizobia interaction (see below), the Yucca-Yucca moth interaction [82] and in humans [83]. In meerkats, pregnant subordinates will kill other young — even those of the dominant — and so the dominant increases the survival of her offspring by harassing and evicting pregnant subordinates [73]. A more complicated possibility is that the punished individuals change their behaviour in response to punishment, and are more likely to cooperate with the punisher in future interactions [84]. The relative importance of such punishment remains a major question — it is at work in cleaner fish and could be important in other cooperatively breeding vertebrates or humans.

Enforcement could also be favoured if it provides an indirect fitness benefit [77,78,85]. The simplest way this could occur is by reducing the fitness of individuals who are competing with relatives and hence freeing up resources for relatives. In some ants, bees and wasps, a fraction of the workers lay their own eggs [86]. Other workers frequently do not tolerate such selfish behaviour and selectively cannibalise or 'police' eggs laid by workers. This behaviour is selected for because the policing workers can be more related to the sons of the queen than to the sons of the other workers and because cheating workers raising their own sons can reduce the colony's overall productivity [87]. Across species, it has been shown that there are higher levels of worker cooperation at which policing is more common and effective. Specifically, the proportion of workers who lay eggs is negatively correlated with the probability of worker laid eggs being killed [86] (Figure 7B). One way of conceptualising this is that policing reduces the fitness gains of cheating, which is the same as reducing the cost (c) of cooperating in Hamilton's rule.

Fixed Enforcement Strategies

The two previous sections emphasise how cooperation can be enforced by conditional enforcement of behaviour in response to the level of cooperation shown by others. However, cooperation can also be enforced with fixed strategies that limit the opportunity for competition or cheating [8,57]. If opportunities for competition or cheating are limited, individuals can only increase their own success by increasing the success of their group [57]. Consequently, any mechanism that aligns reproductive interests or represses competition within groups will select for higher levels of cooperation. Fair meiosis may be an example of such a mechanism, selected for because it aligns the reproductive interests of genes in a genome [8]. Although selfish genes that increase their own transmission rate can arise and spread, there is selection for them to be suppressed by genes elsewhere in the genome [88]. Other examples of mechanisms that may have evolved to reduce conflict within organisms include separating symbionts into reproductive germ line lineages, and

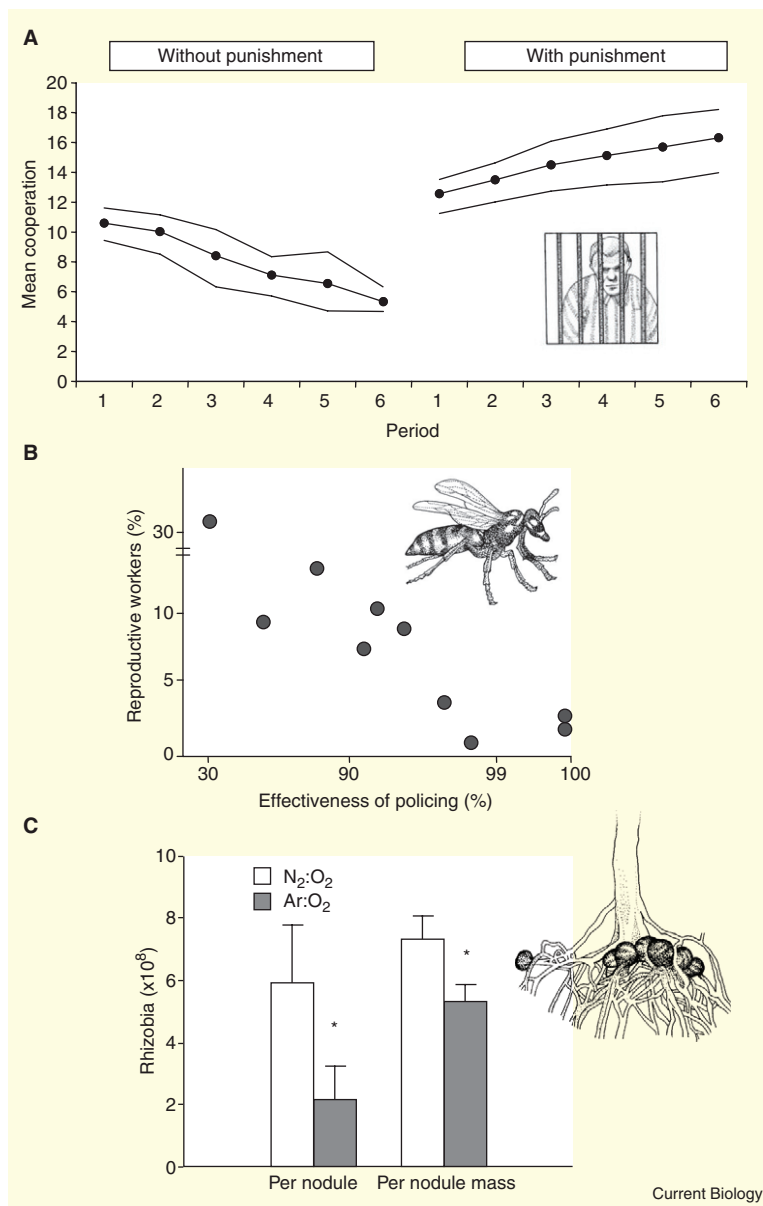


Figure 7. Enforcing cooperation.

(A) Humans show higher levels of cooperation in economic games when there are opportunities to punish individuals who do not cooperate. Reproduced with permission from [74]. (B) Lower levels of worker reproduction (cheating) are observed in wasp and bee species where worker policing is more effective [86]. The effectiveness of policing is measured by probability of worker-laid eggs being killed relative to queen-laid eggs. Reproduced with permission from [86]. (C) Legumes sanction rhizobia bacteria that do not fix nitrogen for them [91]. The plant reduces the oxygen supply to nodules where air (N₂-O₂) is replaced by a gas mixture (Ar-O₂) which contains only traces of nitrogen, thus leading to a decrease in rhizobial growth. Reproduced with permission from [91].

non-reproductive, somatic lineages [89] as well as the uniparental transmission of cytoplasmic genes, such as mitochondrial genes [90].

Things Aren't Always So Simple

Although we have emphasised how the mechanisms favouring cooperation can be divided up, these mechanisms are not mutually exclusive and there is considerable scope for interactions between them. The examples above have demonstrated how punishment or policing can favour higher levels of cooperation due to direct or indirect fitness benefits. Such mechanisms of enforcement cut across the direct-indirect fitness distinction, because they can alter the relative cost and benefit of cooperating — the *b* and *c* of Hamilton's rule [12]. In many cases, both direct and indirect benefits may be involved. For example, if the rhizobia in a root nodule do not provide nitrogen

to their leguminous host plant, the plant reduces the growth rate of the bacteria by decreasing oxygen supply [91] (Figure 7C). In this case, each rhizobium cell is selected to fix nitrogen to avoid both itself and its relatives within the nodule being sanctioned. Another complication is that just as competition between relatives reduces kin selection for cooperation, local competition for resources can also reduce the direct fitness benefits of cooperation [92].

Origin versus Maintenance of Cooperation

It is useful to distinguish between the evolutionary forces favouring the origin and the subsequent elaboration and maintenance of a trait. However, this distinction is rarely made for cooperation. One issue is that the selective force initially responsible for the evolution of cooperation may differ from that driving the observed level of cooperation. In particular, even when there could eventually be a direct fitness benefit

to cooperation, it can be hard or impossible for cooperation to spread initially. This is for instance the case with reciprocity [65], punishment [77,78] and group augmentation [56]. It is, therefore, likely that some level of cooperation may initially arise due to factors such as kin selection or shared interests, and that only after this can punishment or sanctions select for higher levels of cooperation [77]. Analogous arguments have been made for cooperatively breeding vertebrates, social insects and rhizobia [58,81,86]. Another issue is that any mechanism that reduced symbiont diversity would provide a longer term benefit by more closely aligning the reproductive interests of the symbiont with their host [93]. However, this would only be selected for if it provided an immediate benefit. For example, fungus-growing ants in the genus *Acromyrmex* remove new strains of fungi from their nest, because it leads to a costly incompatibility reaction with their resident fungus strain [94]. In an accompanying review in this issue, Boomsma discusses how mating systems can influence the origin and maintenance of cooperation [95].

What We Need

It is more important to start with what we don't need [96]. First, we do not need to keep reinventing the wheel with more theoretical models that incorrectly claim to provide a new mechanism for the evolution of cooperation [12,97,98]. This has especially been a problem with models that examine limited dispersal or group structures [99–103] and which are, therefore, just reinventing kin selection [12,97,98]. If links with existing theory are not clarified, this misleads and causes confusion. This is illustrated by a recent review which suggests five mechanisms for the evolution of cooperation [104] — three of these were just different ways of modelling the same thing (kin selection) [97,105–107], two were different forms of reciprocity, and hence unlikely to be important outside of humans, and most direct fitness benefits for cooperation were ignored. Second, we do not need redefinitions of terms that already have specific and useful meanings. For example the confusion that has been generated by the various redefinitions of 'altruism' since Hamilton's [2] original and extremely useful definition [1].

Third, we do not need more convoluted theoretical analyses of games such as the Prisoner's Dilemma, snow drift, etc. This approach was extremely useful in the 1970s and 1980s for illustrating that cooperation was a problem and provides a useful framework for conducting experiments with humans. However, games such as the Prisoner's Dilemma and its solution with various forms of reciprocity make a large number of extremely specific and often unrealistic assumptions. We now have much more general, powerful and often simpler methods for analysing the evolution of social behaviours [11,108–110]. Furthermore, these other methods allow the biology to lead the mathematics [111], rather than contorting real systems into the form of an artificial game [112,113], and hence facilitate the empirical application and testing of theory. Fourth, we do not need to waste more time on the group selection debate, which was resolved over 20

years ago [10,114]. Group selection is just an alternative way of doing the maths — most workers prefer the kin selection approach because it is usually simpler, more powerful, easier to link with empirical studies and avoids semantic confusion [1].

Now, what do we need? First, we need greater integration between theoretical and empirical work [115]. Much theoretical work is aimed at developing very general models that can be difficult to apply to real systems. A greater emphasis is needed on the development of models that can be applied to and tested in specific systems [53,116]. The usefulness of this approach is clearly demonstrated by the fact that the most successful branches of social-evolution theory, such as sex-ratio evolution, are those where theory and empirical work have been highly integrated [11,22,47,117]. The need for testable predictions is particularly great for many direct fitness explanations for cooperation. In addition, theory is required to make better use of real data, by providing methods for estimating parameters such as the various components of inclusive fitness [118], and the extent to which competition between relatives reduces selection for cooperation [36,119].

Second, the possible advantages of less traditional study systems need to be exploited. Previous empirical work has focused on animals, and within them, the Hymenoptera and the cooperatively breeding vertebrates. Presumably this is because of the complexities offered by haplodiploid genetics, an excuse for birdwatching or the glamour of working with fluffy mammals. Far less attention is applied to other species such as termites [120], social spiders [60] or aphids [121]. The amazing opportunities offered by bacteria and other microbes have only just been realised, let alone exploited [9]. Furthermore, apart from work on selfish genetic elements and their suppressors [88], far less attention has been paid to the problems of cooperation that occupy lower levels among the major evolutionary transitions, such as the evolution of multicellularity [122].

Third, we need greater unification. In some cases, there is surprisingly little interaction between empirical workers and theoreticians who work on different taxa or in different areas. This lack of unification can lead to the semantic and reinvention-of-theory problems discussed above. Inclusive fitness theory [2] provides a relatively unified body of theory on the evolution of cooperation [1,12,32,55,57], and the major aim for the future should be to show how this links and differentiates explanations for cooperation across various taxa and levels of biological organisation.

Fourth, we need to emphasise both the distinction and interplay between mechanistic (proximate) and evolutionary (ultimate or selective value) approaches. It has long been appreciated in the animal behaviour [123] and evolutionary [124] literature that these are complementary and not competing approaches. Indeed, failing to discriminate these approaches can lead to considerable confusion, as illustrated by the recent literature on cooperation in humans [1]. However, this distinction has also led to research on evolutionary questions tending to ignore mechanistic issues. This is a problem when an understanding of mechanism can

help explain the pattern and precision of adaptation [125]. For example, the ability with which ants can recognise kin has been shown to depend upon mechanistic constraints imposed by the cuticular hydrocarbon mechanism underlying this behaviour: ants misestimate how many times their queen has mated when her mates share the same cuticular hydrocarbon profile [22].

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